THE MUSCULATURE OF THE MANDIBULAR AND HYOID ARCHES IN A STING-RAY (*TRIGONORHINA FASCIATA*).

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(*Communicated by Professor A. N. Burkitt.*)

(Two Text-figures.)

[Read 31st July, 1940.]

Vetter (1874) described systematically and thoroughly the "Kiemen- und Kiefermuskulatur der Fische". The muscles described were, mainly, the branchial constrictor sheets and their homologues in the mandibular and hyoid arches.

The constrictors were called superficial constrictors; their dorsal or ventral position and the arch to which they belonged were mentioned, and any further subdivision was shown by the use of Arabic or Greek letters. Such a name as the second ventral constrictor part b is typical of those in use; it was abbreviated to csvb2.

Ruge (1896), Marion (1905), and subsequent writers have adopted this classification.

In 1939 a resurvey of this musculature was made in elasmobranch sharks (Lightoller, 1939), when greater attention was paid to the structure of a typical branchial arch. The constrictor sheet, forming the branchial interseptum, was subdivided into (*a*) P. branchialis which lay between the branchiae, (*b*) P. inscriptionalis which lay caudal to the branchiae but was, likewise, supported by the branchial rays; often it was attached to the lateral ray by an inscription, (*c*) P. arcuata whose fibres were unsupported and passed, without interruption, from the dorsal to the ventral surface of the body. It lay in the free edge of the interseptum and formed a "gill hood".

Several facts were disclosed by this closer survey. In each arch a levator muscle was displayed lying deep to each constrictor sheet; this was sometimes weak, but was powerfully developed in the first (mandibular), second (hyoid), and the caudal arch. The levator and constrictor musculature of the branchial arches was found to be supplied by occipito-spinal nerves. In *Mustelus antarcticus* no branches from the Xth cranial nerve were seen to enter this musculature. Further, the innervation of the P. arcuata was identified; this was, wholly or partially, by fibres from the nerve of supply to the P.p. branchialis and inscriptionalis of the interseptum caudal to it; i.e. by a prebranchial nerve.

The application of these findings to the musculature of the mandibular and hyoid arches led to a clearer understanding of this and a new conception of that. Homologues of the P.p. branchialis, inscriptionalis and arcuata and of the levator sheet were disclosed in the mandibular arch musculature. The P. arcuata (cs1c) was constant ventrally; dorsally it was infrequent. Both were always supplied by the VIIth cranial nerve, i.e. by the nerve innervating the caudally adjacent constrictor sheet of the second (hyoid) arch.

Moreover, the P. arcuata dorsalis (csd1c) always lay caudal to the spiracle owing to the rostral movement of the external opening of this cleft. In the present paper the musculature of the mandibular and hyoid arches of the sting-ray will be similarly described. The ventral position of the gill clefts in Rays and Skates, the lateral thinning of the branchial basket and its attachment to the propterygium have caused modifications in the basic plan of the branchial musculature. Such modifications are, phylogenetically, unimportant and will not be described: they are indicated in the dioptograms. In describing the muscles the abbreviations csv1a, csv2a, etc.[1], will be bracketed after the name of the muscle—thus defining the homology of the muscle.

I. Superficial Constrictor Musculature.

A. *Of the First (Mandibular) Arch.*

In this Ray P.p. "a", "b" and "c" of the hypothesized first constrictor sheet are present. The modified cartilages which form the jaws have, however, divided the original sheet into three groups: a dorsal (cranio-palatal); an intermediate (palato-Meckelian); and a ventral (inter-Meckelian). The part "b" includes the three groups of fibres; parts "a" and "c" have dorsal and ventral, but no intermediate component.[2] The above conditions seem common to all elasmobranchs.

Dorsal Group: This consists of three separated muscles: The P. prae-orbitalis (csd1a), which will be described with the M. adductor mandibulae; the P. cranio-maxillaris (csd1b′) and the P. nucho-maxillaris (csd1c).

P. cranio-maxillaris (csd1b′): This is well developed and, at its origin, consists of three bands of interwoven fibres, two superficial and one deep. It takes origin from the deep surface of the post-orbital process (Po.O) and the lateral wall of the otic capsule. The origins of this muscle interlace with those of the first and second levators (L1 and L2). Soon after its origin a single muscle belly is formed which constitutes the posterior wall and floor of the orbit. It is inserted into the dorsal surface of the concavity of the palato-quadrate, lateral to the middle line. The muscle is innervated by the oto-spiracular branch of the Vth. A deeply situated band of fibres passes between the insertion of csd1b′ and that of the first levator (L1).

P. nucho-maxillaris (Levator rostri, csd1c): This is well developed, though less so than the depressor rostri (csv1c). It takes origin from the sheath of the dorsal longitudinal musculature, extending from the fibrous sheath of the second levator (L2) to the vertical superficial ridge formed by fused transverse processes. Caudally the fibres are closely interlaced with those of the P. epihyoidea (csd2a). The fibres quickly taper to form a fine tendon at the level of the second levator (L2). From here the long tendon skirts the spiracle, crosses the M. adductor mandibulae—lateral to the orbit—and the root of the pre-orbital process; it ends in the free margin of the rostral region medial to the propterygium. There is a thin tendon sheath. The course of this tendon mirrors that of the M. depressor rostri (csv1c). The innervation is from the VIIth (indicated on the left side of Fig. 1). In the sharks the P. nucho-maxillaris (csd1c) was always inserted into the cartilages of the jaws, though the P. mandibularis (csv1c) frequently ended

[1] This is a slight variation in the order of the letters suggested by Vetter.

[2] The dorsal "a" fibres are not attached to the palato-quadrate, but pass, as in other elasmobranchs, from the skull to the lower jaw without interruption. Strictly speaking, intermediate "a" fibres are included with the dorsal "a" group. See Lightoller, 1939, Pl. i, fig. 1.

upon the surface of the M. adductor mandibulae. In the rays the dorsal, as well as the ventral, muscle has acquired a similar specialized insertion.

Intermediate Group: Two muscles will be described in this group, the P. prae-orbitalis (csd1a) and the P. quadrato-mandibularis (cs1b″). They form a functional unit—the M. adductor mandibulae.

P. prae-orbitalis (csd1a): A small but well developed muscle; it is seen only in the ventral dioptogram. The origin is by a broad, thin, tendinous sheet from the base of the skull, caudo-medial to the nasal capsule. Passing ventro-caudally, the flat muscle belly lies ventral to the P. quadrato-mandibularis; it ends in a laterally compressed tendon which is inserted into the ventral surface of the mandible (Fig. 2).

P. quadrato-mandibularis (cs1b″): The muscle is a complex one. Like that of *Heterodontus* it has no lateral raphe and its dorsal and ventral portions are discrete. The *dorsal fibres* (csd1b″) form three muscle bellies. The caudal belly takes origin from the caudal end of the palato-quadrate; its superficial fibres end by interlacing, at right angles, with those of the intermediate belly or by being attached to the pre-orbital process; its deeper fibres are inserted into the caudal end of the mandible. Some fibres from the caudal end of the mandible, also, are attached to the pre-orbital process (Figs. 1 and 2). The intermediate belly takes origin from the palato-quadrate rostral to the caudal belly. All its fibres end in the pre-orbital process. The rostral belly takes origin from the nasal capsule; all its fibres are inserted into the pre-orbital process.[3]

The ventral fibres (csv1b″) form two muscle bellies; at first sight there appear to be three, owing to the superficial position of the tendon and belly of the P. prae-orbitalis (csd1a). The large lateral belly takes origin from the ventral surface of the mandible rostral to the attachment of the caudal fibres of the P. inter-mandibularis (csv1b′). The insertion is a very extensive one and lies hidden, to some extent, by the P. prae-orbitalis (csd1a). A few fibres end at the angle of the mouth. The remainder are inserted into the ventral surface of the palato-quadrate, extending from an area medial to the angle of the mouth to the lateral free end of the palato-quadrate (Fig. 2).

The medial belly takes origin from the ventral para-median plane of the lower jaw by a long thin tendon which becomes muscular near the angle of the mouth. A few fibres are attached to the angle of the mouth; the remainder join the deep surface of the lateral ventral belly of the M. adductor mandibularae (Fig. 2). The M. quadrato-mandibularis is innervated by the Vth.

Ventral Group: This consists of three muscle sheets. The two rostral ones form the P. intermandibularis (csv1a′ and b′); the caudal muscle is the P. mandibularis (depressor rostri, csv1c).

P. intermandibularis (csv1a′ and b′): These two muscles help to form the diaphragm of the floor of the mouth. The rostral muscle (csv1a′) takes origin from the concave surface of the mandible close to the middle line and for a short distance lateral to this. The fibres pass obliquely towards the middle line, soon become tendinous and interlace freely with each other and with the fibrous sheet which covers the ventral longitudinal musculature.

The caudal muscle (csv1b′) takes origin from the ventral fascia and is inserted into the ventro-lateral surface of Meckel's cartilage.

[3] This muscle is shown, but not labelled in Fig. 1.

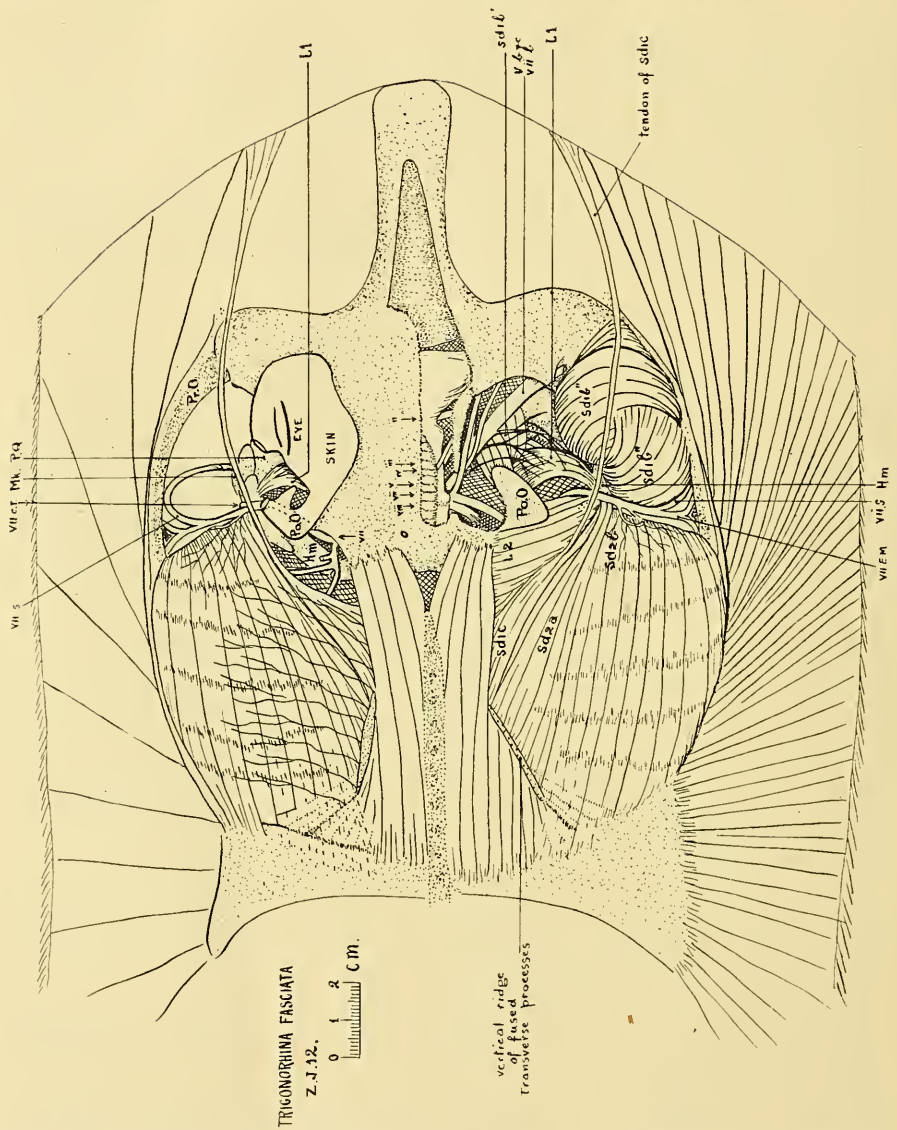

Fig. 1.—*Trigonorhina fasciata*; dorsal view; × ½. On the left side the P. quadrato-mandibularis, the second levator and the lateral wall of the spiracle have been removed. On the right side the eye and its musculature, the dome of the skull and of the otic capsule have been removed. On this side the N.n. otospiracularis and prespiracularis are shown as black lines crossing the orbital cavity.

In both figures the lateral fins have been severed close to the propterygium—though this is not figured. Both figures are dioptograms.

Hm, hyomandibula; *L1*, *L2*, first and second levators; *Mk*, Meckel's cartilage; *Po.O* and *Pr.O.*, post and prae-orbital processes; *P.Q.*, palato-quadrate; *sd1a*, P. prae-orbitalis; *sd1b'*, P. cranio-maxillaris; *sd1b''* and *sv1b''*, P. quadrato-mandibularis; *sd1c* and *sv1c*, levator and depressor rostri; *sd2a*, P. epihyoidea; *sv1a'* and *sv1b'*, P. intermandibularis; *sv2a*, P. interhyoidea; *sd2b* and *sv2b*, P.p. inscriptionalis; *sv2c*, P. arcuata ventralis forming the gill hood; *V.b.* and *c*, and *VIIb*, b and c divisions of the Vth and VIIth cranial nerves; *V. Mhy*, mylohyoid branch of the Vth; *VII C.T.*, chorda tympani; *VII E.M.*, external mandibular branch of the VIIth; *VII S*, symphyseal or mandibular branch of the VIIth.

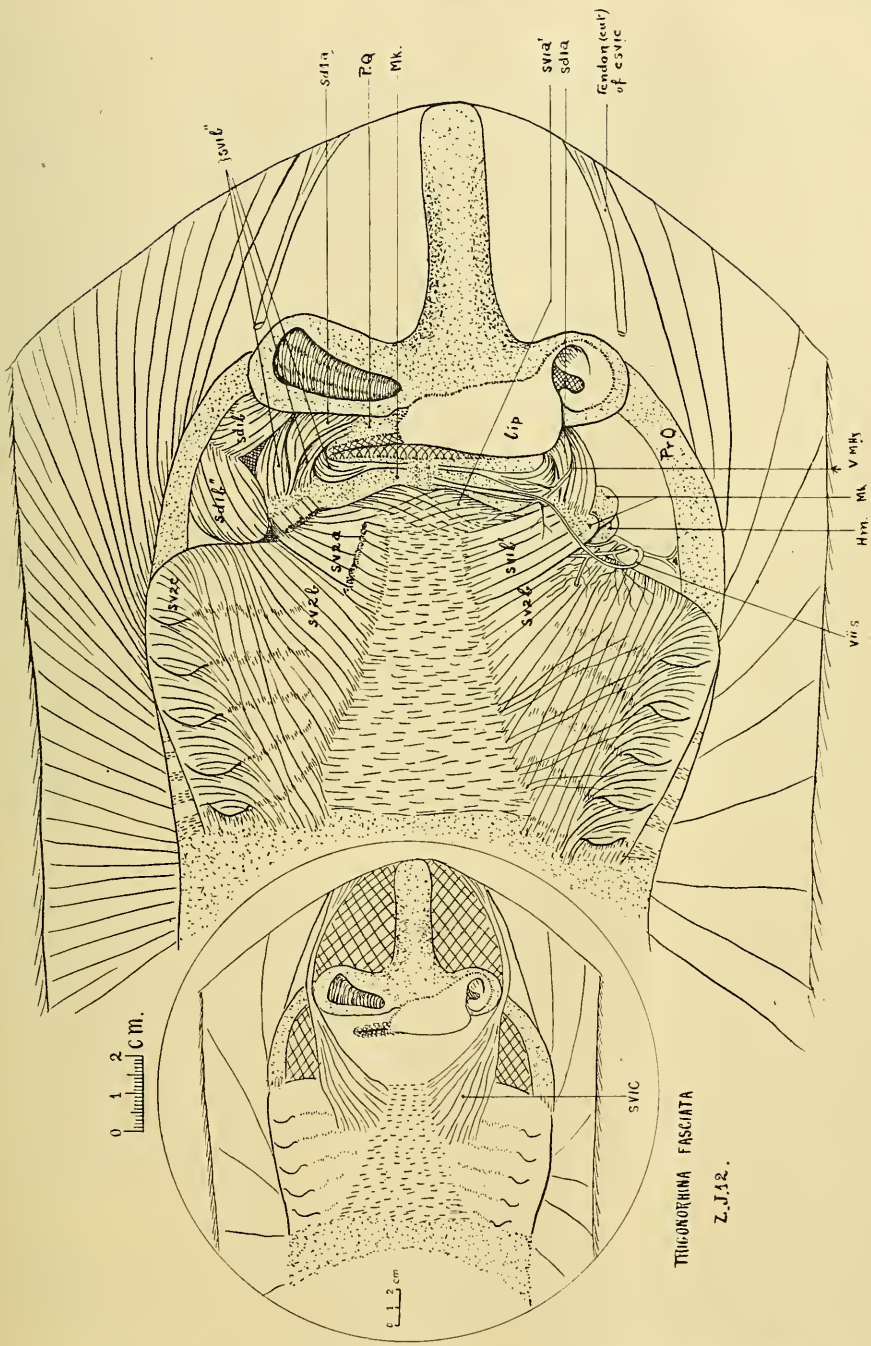

Fig. 2.—*Trigonorhina fasciata*; ventral view, × ½. On both sides the depressor rostri has been removed, but both are shown in the inset (× ¼). On the left side the P. quadrato-mandibularis has been removed. On the right side the upper lip, the covering of the nasal capsule and part of the P. intermandibularis (sv1b′) have been removed. Note the chorda tympani (unlabelled) curling around the neck of the hyomandibula, and the symphyseal branch of the VIIth (VII S) crossing superficial to the mylohyoid branch of the Vth (V.Mhy).

Both these muscles are innervated by the mylohyoid branch of the Vth which lies upon their superficial surface (Fig. 2). The caudal muscle is also supplied by a twig from the VIIth which enters its deep surface (Fig. 2).

P. mandibularis (M. depressor rostri, csv1c) (Fig. 2, inset): This muscle takes no part in supporting the floor of the mouth; it is larger than the M. levator rostri (csd1c). It takes origin chiefly from the fibrous sheet which covers the ventral longitudinal musculature; medially and caudally the fibres are inextricably interlaced with those of the csv1b′, csv2b and branchial musculature. Its fibres converge towards the base of the pre-orbital process passing ventral to the lateral end of Meckel's cartilage and the M. adductor mandibulae. Before reaching the base of the pre-orbital process the muscle fibres are replaced by a stout tendon which runs in a definite sheath. The tendon ends in the free margin of the rostral region medial to the propterygium and immediately ventral to the tendon of the levator rostri (csd1c). A few fibres separate from the muscle belly and form a fine tendon which ends in the angle of the mouth. The muscle is innervated by the VIIth (Fig. 2).

B. *The Superficial Constrictor of the Second (Hyoid) Arch.*

Like the constrictor of a branchial arch, this consists of dorsal and ventral groups; some of the parts into which each of these is subdivided have acquired functional independence.

P. epihyoidea (csd2a): As in *Orectolobus* the muscle is not large enough to cover the second levator (L2). It takes origin from the vertical ridge of the fused transverse processes and from the tendinous aponeurosis separating the second and third arch musculature. Passing rostrally the fibres form a musculo-tendinous sheet which winds around the distal end of the second levator (L2). It gains insertion into the neck of the hyomandibula ventro-lateral to the insertion of the second levator. It is innervated (Fig. 1, left side) by the first extra-cranial branch of the VIIth; this is deeply placed and supplies also the second levator (L2) and the levator rostri (csd1c).

P. interhyoidea (csv2a): As in the sharks, this lies deep to the csv1b′ fibres of the P. intermandibularis. The majority of the fibres take origin from the ventral fascia in common with the fibres of csv1b′, but a few take origin, anterior to this muscle, from the surface of the csv1a musculature. Owing to the poor development of the cerato-hyoid the insertion is unusual. The most superficial fibres pass caudal to the Meckelo-hyomandibular ligament and fuse with the rostral ends of the csd2b and csv2b fibres; some fibres pass deep to this ligament to be inserted into the head of the hyomandibula; the remainder of the fibres are inserted into the cerato-hyoid. The muscle is innervated by the same branch of the VIIth which supplied the csv1b′ fibres of the P. inter-mandibularis.

P. inscriptionalis (csd2b and csv2b): No inscription was seen separating these two muscle sheets; their fibres appear to interlace on the rostral margin of the branchial basket. Both sets of fibres are supplied by the VIIth.

P. arcuata (csd2c[1] and csv2c): The dorsal fibres cover the lateral portion of the branchial basket, but take no part in the formation of the gill hood. This is formed by the csv2c fibres. At the lateral margin of the branchial basket the muscle fibres become fibrous and cannot be traced accurately. The nerve supply of the P. arcuata was not determined.

[1] Not indicated in the dioptogram.

II. Levator Musculature.

First levator (L1): This is a well developed muscle which supports the rostral wall of the spiracle. It takes origin from the lateral surface of the otic capsule where its fibres are interlaced with those of the P. cranio-maxillaris (csd1b′). The fibres are inserted into the lateral end of the hyomandibula (Fig. 1, both sides). It is innervated by the oto-spiracular branch of the Vth.

Second levator (L2)[5]: This is a powerful superficial muscle; it is enclosed in a thin, but strong fibrous compartment which isolates it from the P. epihyoidea (csd2a) and the levator rostri (csd1c). It takes origin, chiefly, from the cartilagincus skull, but some fibres take origin from the fibrous sheath of the dorsal longitudinal musculature. It is inserted into the greater part of the dorsal surface of the hyomandibula, extending almost to the insertion of the P. epihyoidea (csd2a). It is innervated by the first extra-cranial branch of the VIIth—which lies deep to the muscle.

Summary.

A brief account has been given of the musculature of the mandibular and hyoid arches in a ray. Individual muscles have readily been homologized with those found in the elasmobranch sharks. No unfamiliar muscles were found though some were highly specialized. The apparently complete homology of the musculature of the first (mandibular) arch with that of a branchial arch in this ray is in conformity with that recently described by the author for other elasmobranchs.

Acknowledgements.

In conclusion I wish to thank Professor Burkitt of the Department of Anatomy for his continued interest and help; the Department of Anatomy, University of Sydney, for facilities for work and for material; Miss E. C. Pope, Miss M. Hutley, and the Department of Zoology for additional material and the branchial skeleton of a ray.

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[5] Parker and Haswell (*Text Book of Zoology*, ii, 1897, p. 160) figure the skeleton of a sting-ray.